

The Effects of Population Density on Patterns of Resource Utilization by Yarrow's Spiny Lizard*

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ABSTRACT

The influence of population density on patterns of resource utilization was examined using small enclosed populations of adult *Sceloporus jarrovi* in which density was varied from normal to four times normal. Censuses of active lizards were conducted three times per day; location, time, perch substrate, perch light condition, perch height, and perch diameter were recorded for each lizard. Stepwise multiple discriminate analysis revealed differences along time and perch gradients. At higher densities, animals were active throughout the day and spent more time in the shade and less in the sun. At higher densities, they shifted perch substrate selection from normally-preferred rock substrate to log and ground substrates. Significant differences among density groups were not found in selection of perch height or diameter. The observed differences in patterns of resource utilization may act to reduce the effects of competitive interactions since no significant differences in weight gain among groups were observed.

The importance of behavioral studies for ecology is evident in recent plethora of articles and books concerned with such studies.^{1,2} Many of these writings focus on how animal inter-relationships often affect patterns of resource utilization and the converse, how resources affect the ways animals relate to one another. As shown by many recent publications, the behavior of animals is closely tied to their ecology. While behaviorists generally focus on the behaviors exhibited by individuals and ecologists on the behaviors exhibited by a species, behavioral ecologists focus on the impact individual flexibility has on ecolog-

ical processes. Ecologists, for instance, usually define a species' role in its community by focusing on patterns of resource utilization. Two different, general approaches are used: comparisons of different populations and manipulations of the same population. Comparisons of geographically distinct populations reveal the effects of resource availability,^{3,4} seasonality,^{5,6} and community composition^{7,8} on resource utilization patterns. Experimental manipulations of local populations show that both interference and exploitative competition influence utilization patterns.⁹⁻¹³ Crowell¹⁴ and Roughgarden¹⁵ have suggested that population density should influence utilization patterns. Studies by McClure,¹⁶ Whitham,¹⁷

*Sauria: Iguanidae

and Alford and Crump¹⁸ have addressed the effects of density, but have only examined distribution effects. In this paper I shall show that population density affects a number of other aspects of patterns of resource utilization as well.

Traditionally, the dimensions of food, space, and activity time are used to define lizard niches. Measurements include activity time, perch substrate, perch height, perch diameter, and perch light condition. Intensive investigations¹⁹⁻²¹ of patterns of resource utilization by *Sceloporus jarrovi* show that these lizards partition food, space, and time on the basis of size and sex. Alterations in the availability of food^{22,23} and in the thermal environment^{24,25} result in adjustments in activity time and perch site selection. Such flexibility makes this species ideal for studying the effects of population density. By varying density of populations one can assess changes in patterns of resource use. In 1976, I tested the hypothesis that variations in density would have no effect on patterns of time and space utilization by lizards. Since direct assessment of density effects on food selection would have involved killing the animals or handling them excessively, I assessed the density effects on this dimension indirectly by examining changes in their weight over the duration of the study. Here, I hypothesized that the limited availability of food for animals at high density would result in alterations in their patterns of resource utilization; if it did not, animals at high density should show less weight gain than animals at low densities. I tested this the following year and showed that animals in high-density populations (3.5 times normal) given supplementary food gained significantly more weight than unsupplemented animals at the same density.²⁶

Methods

During the summer of 1976, four populations of *Sceloporus jarrovi* were placed in 17-x-17-m enclosures constructed of poly-

ethylene plastic.²⁷ One of four density conditions was randomly assigned to each enclosure: normal, 2X, 3X, and 4X. Areas the same size as each enclosure normally support approximately four individuals (two males and two females with overlapping territories between the sexes); densities thus ranged from four to 16 animals per enclosure or about 138 to 554 lizards per ha.

The four enclosures were located adjacent to one another and did not differ appreciably in general appearance. In each enclosure I mapped all rocks, logs, and trees. Since *S. jarrovi* normally perches on large rocks or rock piles, I assessed the availability of these sites in each enclosure and, where necessary, constructed artificial sites such that the number available in each enclosure was equal.

Adult *S. jarrovi* (Snout-vent length > 50 mm) captured from nearby areas were individually sexed, measured, toe-clipped, paint-marked, and assigned randomly to the enclosures with the restriction that there be an equal sex ratio of different-sized lizards. During the study, a few lizards either escaped or died, so they were replaced by animals of the same sex and approximately the same size. Because of time constraints, sufficient data were not collected on some of these animals; therefore, they were excluded from the analyses.

Data collection. Activity censuses were made at different times throughout the day from mid-July to mid-August such that all portions of the day were equally covered. During each census, a search was conducted in every enclosure. Time, location, perch substrate, height, diameter, and light condition were recorded for each active, i.e. visible, animal. Depending on the number of animals spotted, the procedure took from 10 to 45 min. Because animals became accustomed to my presence and were quite visible, I feel certain that few active animals were missed.

The data for each individual were summarized following the format listed below:

1. Substrate. The relative frequency of association with each of the following

- substrate categories was determined: rock, tree, ground, and log.
2. Light condition. The proportion of time spent in each of the three following categories was calculated: sun, filtered sun, and shade.
 3. Time of activity. The frequency of activity within each of the following time periods was determined: 0800–1100, 1100–1300, and 1300–1600 hours. Proportions for 1, 2, and 3 were normalized using an arcsine transformation.
 4. Perch height. Average perch height was determined, excluding all ground observations.
 5. Perch diameter. The diameters of all perches utilized by lizards were averaged for all substrates, except the ground.

Data analysis. To identify the variables significantly affected by population density, analysis of variance was run as the first step of the discriminant analysis. The data were then analyzed using stepwise multiple discriminant analysis (SPSS).²⁸⁻³⁰ This method allowed for testing of the overall difference among several group centroids. Overall differences among the four densities were tested using Wilks' Lambda statistic. This statistic allows the testing of equality of group centroids and is often converted to the equivalent F or X^2 value. When, and if, significant differences are found, one may then examine the directions of these differences and the variables which contribute to the differences. The method enables the development of a set of variables that can be used to predict group membership and provides a profile of characteristics for distinguishing between groups.

The basic assumptions of multiple discriminant analysis are that variables exhibit multivariate normal distribution and that equal variance-covariance matrices exist between groups.³⁰ Green³¹ notes two further assumptions: one, the groups must be defined a priori and, two, the postulated orthogonal discriminant functions are lin-

ear functions of the original correlated parameters. In this study, groups were defined a priori and original parameters transformed to minimize nonlinearity and improve normality. However, because of the categorical nature of several of the variables, it was necessary to summarize the data for each individual. As a result, for some groups the number of variables exceeded the number of individuals in the group. Thus, the final data matrix could not be tested for homogeneity of covariance and could result in a violation of one of the assumptions mentioned above. Because the test is very robust, the assumptions may be violated. As Green³¹ states with respect to situations of this type, the assumption of homogeneous within-group matrices is unlikely to be satisfied with ecological data, but if the overall test is highly significant, if the discriminant function coefficients are ecologically interpretable, and if distinct separation occurs among the groups on each discriminant function, then it is reasonable to conclude that the differences are greater than would be produced by drawing random samples from a multivariate swarm.

Results

Analysis of variance indicated significant differences among groups for 58.3% (7/12) of the variables (Table 1). Examination of light condition, activity time, perch height, and perch diameter revealed that differences in resource utilization patterns changed markedly as density increased. Significant differences existed among the four densities with regard to substrate use (Figure 1). Animals at higher densities were observed to shift from rock substrate to tree, log, and ground substrate. At normal density animals were observed on rocks almost 100% of the time, while at 4X animals were observed on rocks less than 50% of the time. Utilization of the three different light conditions also changed as density increases (Figure 2). Animals at high densi-

Table 1.—Univariate F values for each of the discriminant variables.

Variable	Univariate F	Significance Level ⁺
Rock	9.137	***
Tree	3.103	*
Log	6.628	**
Ground	6.128	**
Sun	9.036	***
Filtered Sun	2.033	
Shade	6.362	**
Perch Height	2.910	
Perch Diameter	2.320	
Morning Activity	3.394	*
Midday Activity	0.171	
Afternoon Activity	1.509	

⁺ Degrees of freedom: 3 and 28.

* $p = 0.05$; ** $p = 0.01$; *** $p = 0.001$.

ties were observed more often in shade and filtered sun and less often in full sun than animals at normal density. However, significant differences were observed only for sun and shade conditions. Perch height and

perch diameter selection showed no significant differences. While significant differences among the groups were observed only for morning activity, the patterns of daily activity appear quite different (Figure

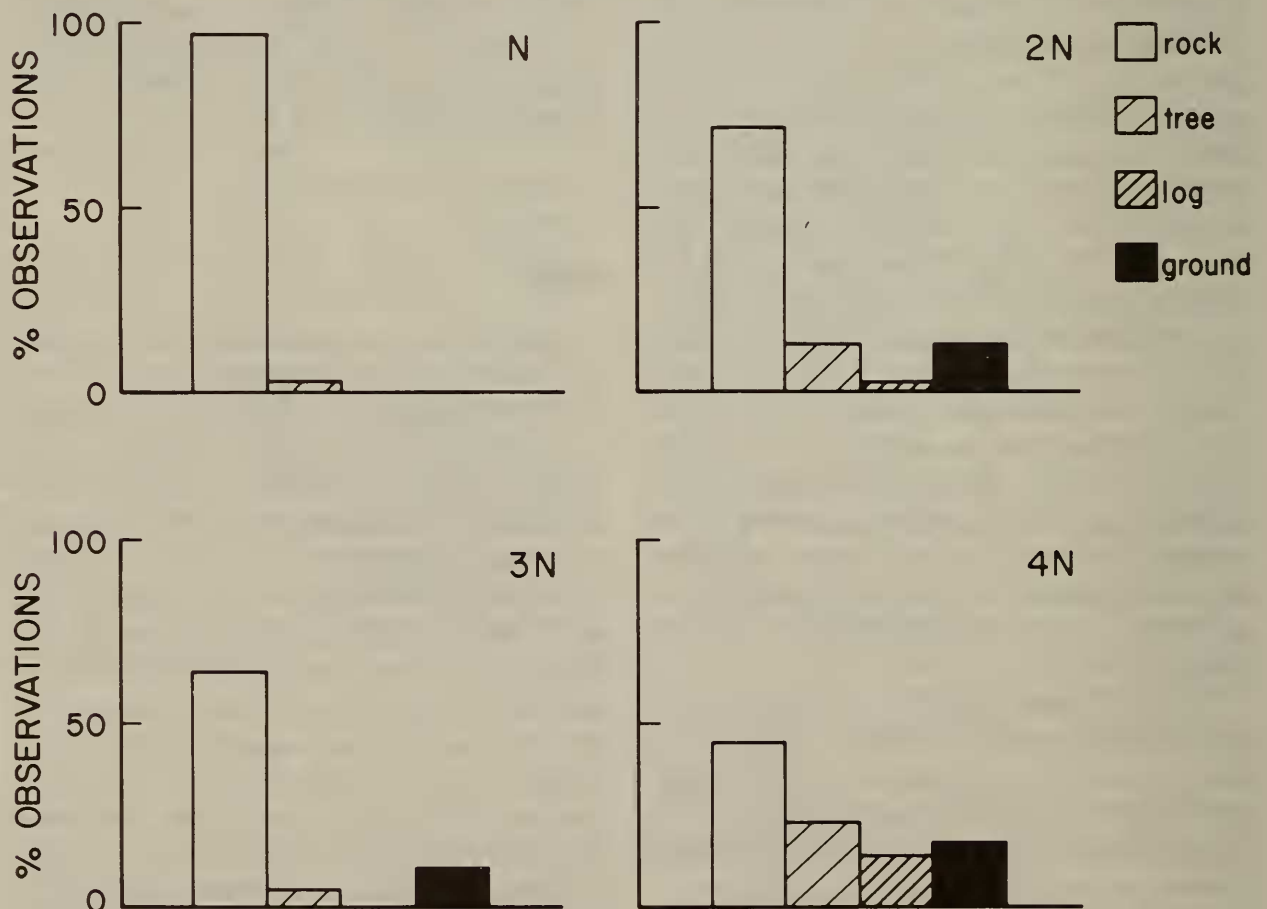


Fig. 1. Mean percent observations of individual *Sceloporus jarrovi* on different substrates as a function of density level.

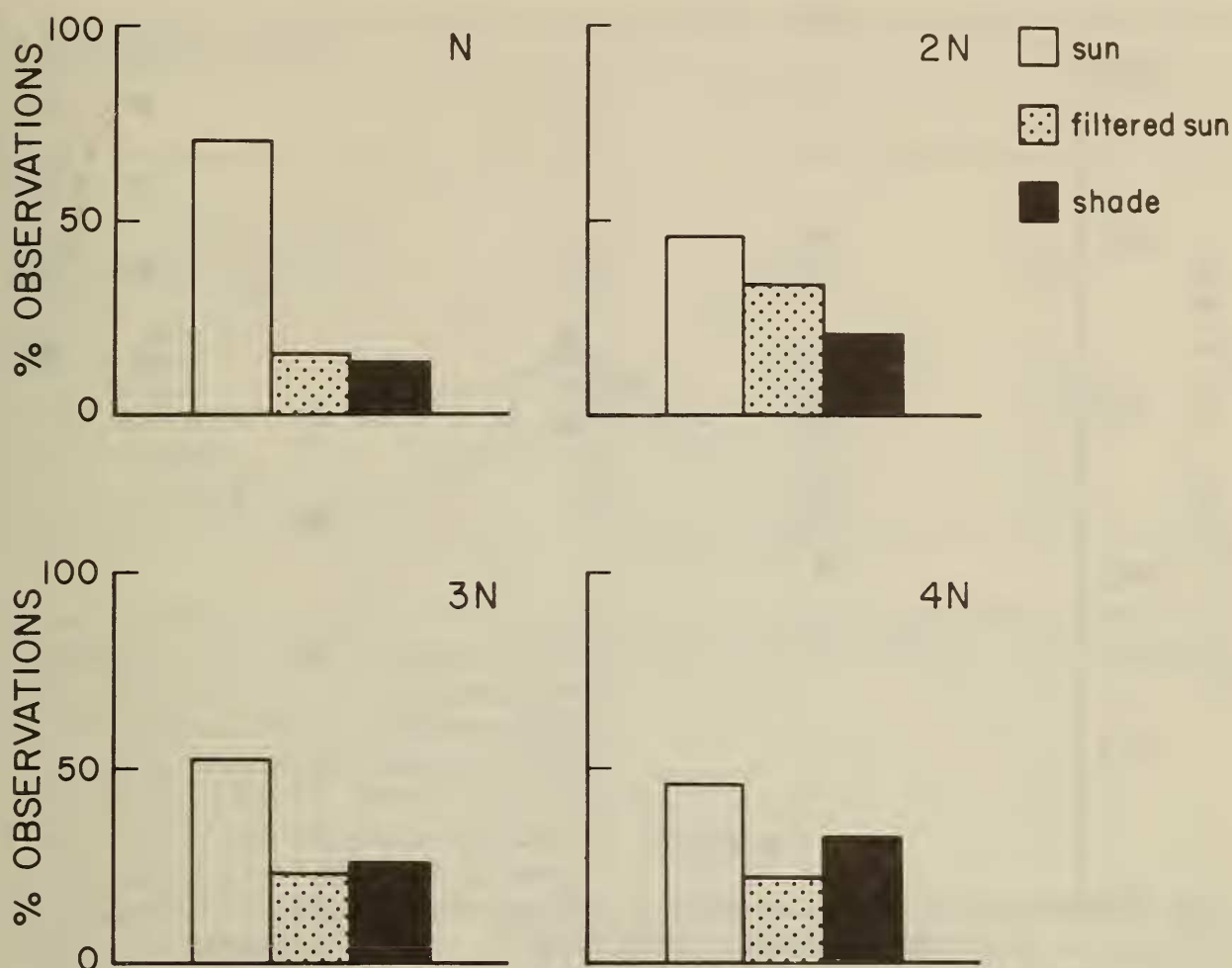


Fig. 2. Mean percent observations of individual *Sceloporus jarrovi* in different light conditions as a function of density level.

3). At higher densities activity was even throughout the day, as opposed to the "peaked" activity observed at normal density.

The measured variables significantly discriminate among the different densities; Wilks' Lambda was calculated to be 0.0862 and is equivalent to an F value of 5.02 with 18 and 65.54 degrees of freedom. The probability of obtaining such an F value is <0.0001 . The untransformed means and standard deviations for each variable at each density are shown in Table 2.

The first discriminant function (DF1) accounts for 57.4% of the relative variability among the densities (Table 3). This function seems to reflect both perch selection and thermal influences as it is primarily formed from the rock and shade variables, as seen by the weighting factors or standardized discriminant function coeffi-

cients (d_i 's) for the variables. Separation is achieved because animals at normal density spend more time on rocks and less time in the shade than those at higher densities, particularly at the highest density.

An additional 28.6% of the relative variability was accounted for by the second discriminant function (DF2) which centered on thermal influences, as seen by the large contribution of the sun variable in the weighting coefficients (Table 3). Separation along this function was complex, as perch diameter, morning activity and afternoon activity were also influential. Animals at normal density were seen in the sun more often than those at higher densities. Note that normal density animals concentrated their activity during the midday period (Figure 3); because of low density, these animals may have been able to move about more easily and, thus, thermoregu-

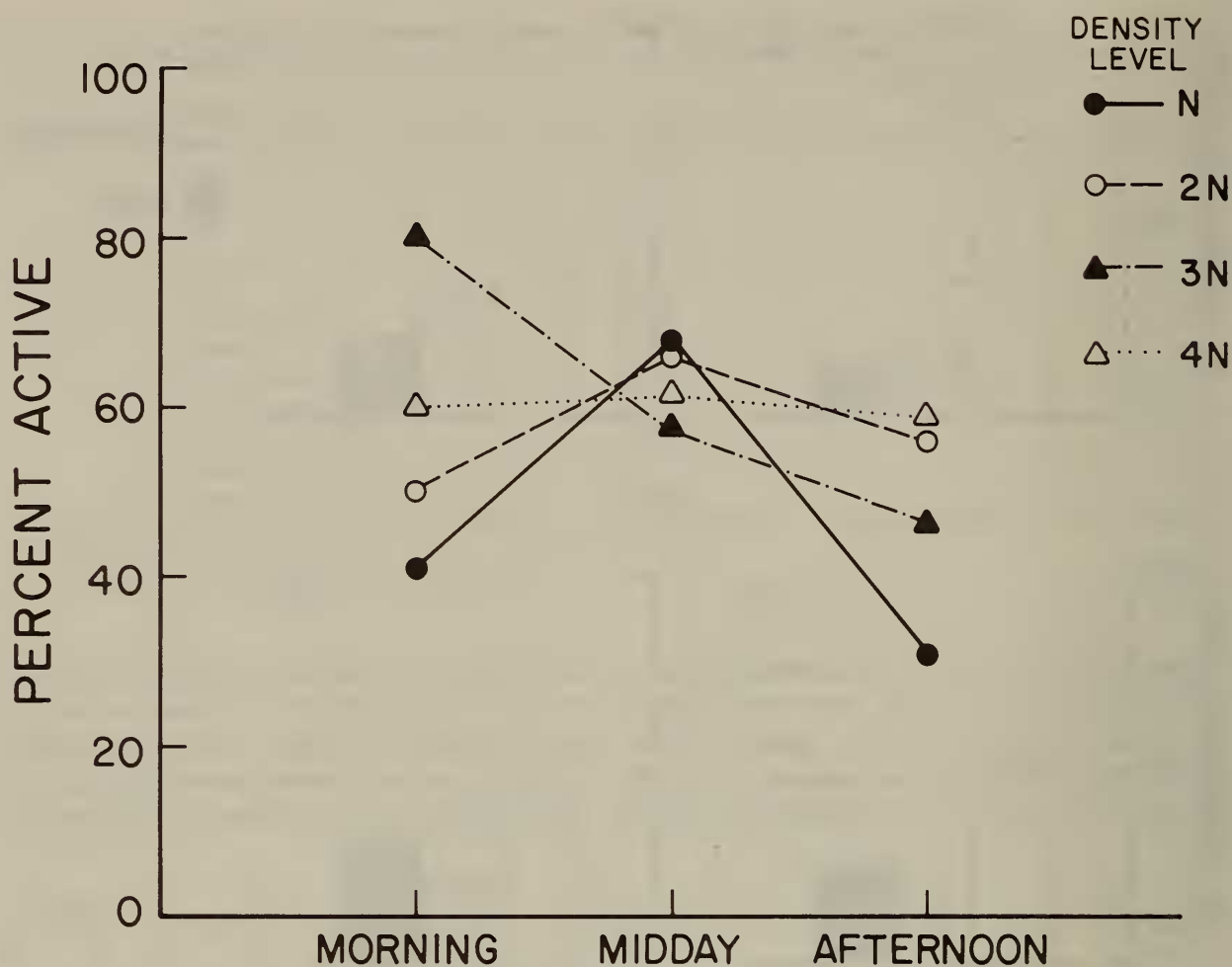


Fig. 3. Mean percent activity of individual *Sceloporus jarrovi* as a function of density.

Table 2.—Untransformed means of the microhabitat variables for each density level. Mean and one standard deviation, in parentheses, are indicated. All refer to unit fractions unless otherwise indicated. Activity is measured as percent population active during the census period.

Variable	Density Level			
	Normal	2X	3X	4X
Rock	0.97(0.06)	0.72(0.18)	0.64(0.13)	0.45(0.25)
Tree	0.03(0.06)	0.13(0.21)	0.05(0.13)	0.23(0.17)
Log	0(0)	0.02(0.03)	0(0)	0.14(0.15)
Ground	0(0)	0.13(0.12)	0.11(0.08)	0.18(0.11)
Sun	0.70(0.09)	0.46(0.10)	0.52(0.07)	0.46(0.09)
Filtered Sun	0.16(0.10)	0.33(0.09)	0.23(0.09)	0.22(0.13)
Shade	0.14(0.01)	0.21(0.09)	0.25(0.11)	0.32(0.08)
Height (meters)	0.32(0.11)	0.29(0.06)	0.28(0.07)	0.46(0.21)
Diameter (cm)	0.38(0.11)	0.31(0.08)	0.32(0.05)	0.40(0.09)
Morning Activity	0.41(0.21)	0.50(0.21)	0.80(0.25)	0.60(0.22)
Midday Activity	0.68(0.14)	0.66(0.21)	0.58(0.20)	0.62(0.29)
Afternoon Activity	0.31(0.10)	0.56(0.09)	0.47(0.22)	0.58(0.29)
Sample Size	4	6	6	16

Table 3.—Standardized discriminant function coefficients (d,'s) showing the relative contribution of the variables to each discriminant function.

	Discriminant Functions		
	1	2	3
Percentage of among groups variance	57.42	28.65	13.93
Cumulative percentage	57.42	86.07	100.00
Variables:			
Rock	-0.753	0.072	-0.205
Sun	0.194	-1.165	-0.344
Shade	0.795	-0.402	-0.545
Diameter	0.358	-0.742	-0.420
Morning Activity	-0.172	0.647	-1.046
Afternoon Activity	0.572	-0.636	0.518

late more efficiently. Greater activity in the morning and afternoon periods occurred at higher densities (Figure 3) which explained the contribution of these variables to DF2.

The third discriminant function (DF3) accounted for a further 13.9% of the relative variability and was primarily a function of activity time. Differences for morning and afternoon activity followed the pattern noted for DF2.

Based on the results of the discriminant analysis, approximately 84.4% of all animals were correctly classified (Table 4). The most distinct group was normal density with 100% correct classification, while even the least distinct groups, 2X and 3X, showed 66.7% correct classification. The locations of the centroids for each of the four densities on the first two discriminant axes are shown in Figure 4.

Weight changes among the four densities

were not significantly different (ANOVA, $F = 1.49$, $df = 3, 28$, $p > 0.05$, Figure 5).

Discussion

Patterns of resource utilization were clearly affected by population density. This alteration was generally characterized by shifts at higher densities. For instance, animals shifted substrate use from the normally-preferred rock substrate to log, tree and ground substrates. A shift in perch light condition at high densities resulted in increased numbers of animals in filtered sun and shade conditions. Not only were animals observed more often in partial sunlight, but they spent more time in these light conditions than animals at low densi-

Table 4.—Classification results of the discriminant analysis for density using microhabitat variables. Numbers in parentheses represent the actual number of individuals placed in each group. The total percent of individuals correctly classified for all groups was 84.4. Sample size does not reflect density due to deaths and escapes (see text for further details).

Actual Group Membership (density)	n	Predicted group membership (%)			
		Normal	2X	3X	4X
Normal	4	100.0(4)	0.0(0)	0.0(0)	0.0(0)
2X	6	16.7(1)	66.7(4)	0.0(0)	16.7(1)
3X	6	0.0(0)	16.7(1)	66.7(4)	16.7(1)
4X	16	0.0(0)	6.2(1)	0.0(0)	93.8(15)

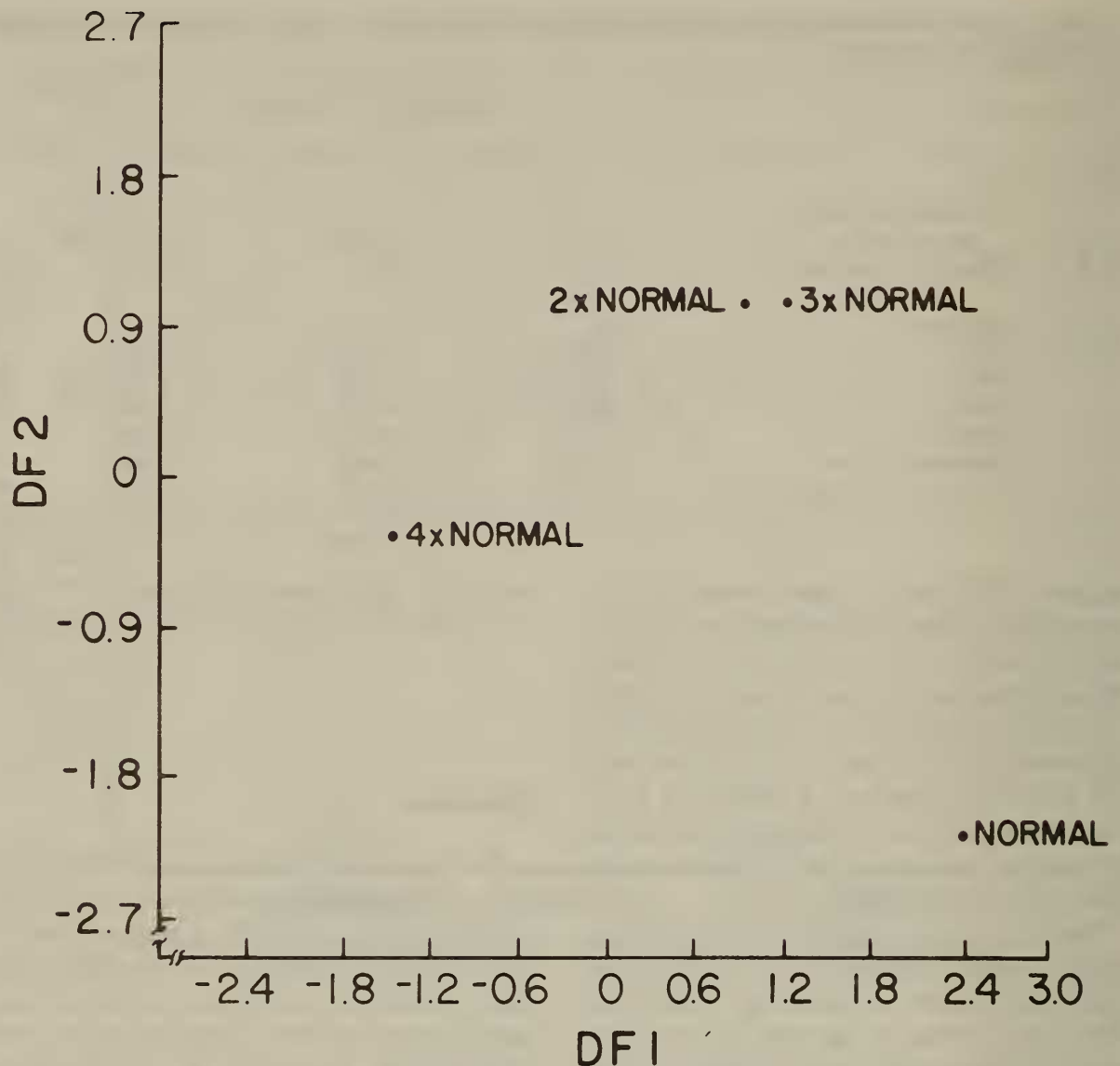


Fig. 4. Centroids of different density groups on the first two microhabitat discriminant axes.

ties.²⁵ These observations, when coupled with the increased activity throughout the day at high densities, suggest that some of the changes in perch substrate and light condition selection might be due to an increased heat load. Burns²⁴ reported a shift in perch substrate selection by *S. jarrovi* in response to changing thermal stresses associated with afternoon activity; animals moved to higher perches in trees to increase convective heat loss. Other studies reporting changes in activity time by *S. jarrovi*^{21,23} show little change in perch substrate selection; none of the changes in activity time, however, were as marked as those observed in this study.

Perch selection with regard to diameter

and height showed no significant differences in response to changes in density. Although other studies of *S. jarrovi* have shown alterations in perch height as a function of food availability,²³ the present results suggest that perch utilization patterns are relatively insensitive to alterations in population density.

The absence of significant differences in weight gain for the animals in the four densities strongly suggests that lizards at high density alter their patterns of food utilization. Normally, *S. jarrovi* forage early in the morning and have full stomachs by about 1100 hours,²⁰ suggesting that the increased activity in the morning and afternoon by high-density animals may allow

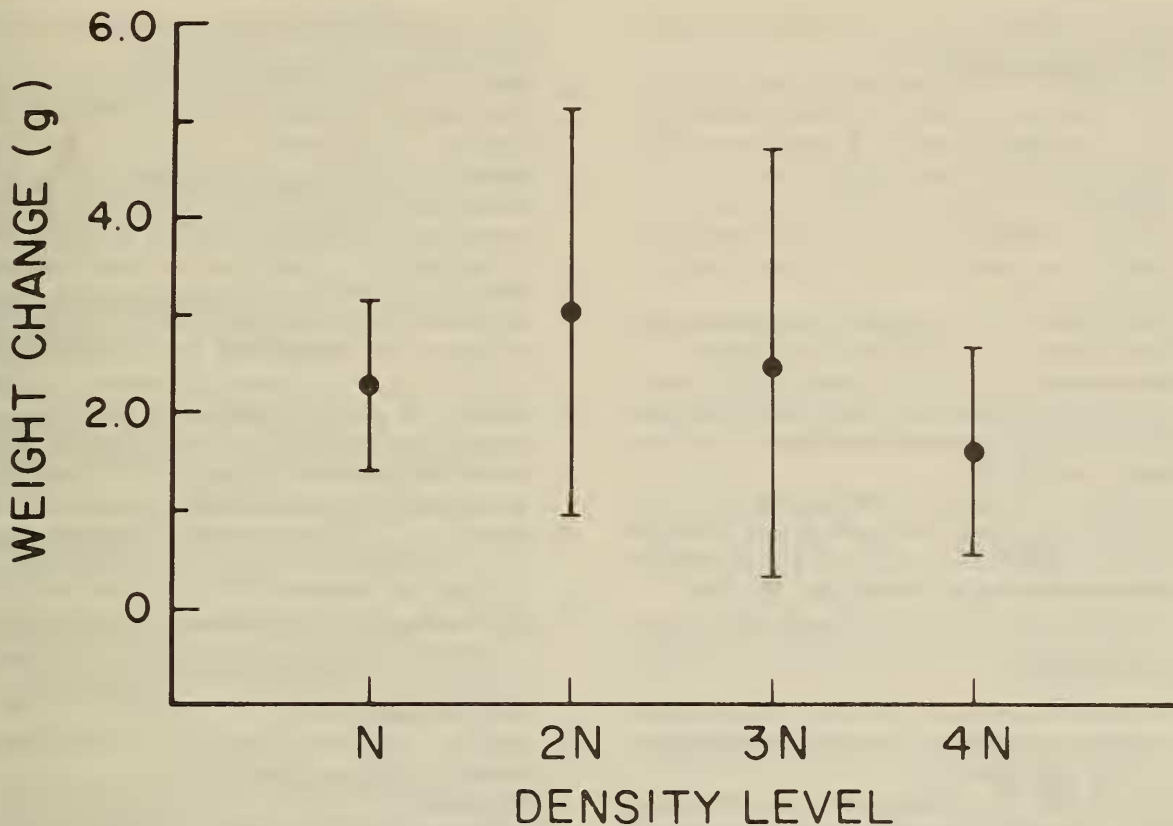


Fig. 5. Weight changes of *Sceloporus jarrovi* as a function of density level. The means and one standard deviation are indicated.

them to forage throughout the day and thereby obtain enough food. Their alterations in perch substrate and perch light condition selection may act to reduce thermal stresses associated with day-long activity and thus allow the animals to remain active.

Clearly the behavioral flexibility exhibited by *S. jarrovi* aids in adjusting the animals to potentially stressful situations. To say that such behavior is adaptive would not, in this case, be presumptuous; alterations in patterns of resource utilization to increased densities up to four times normal that result in non-significant differences in weight gains over a 6-week period must be adaptive.

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ERRATA

In Volume 74, Number 1 of the Journal, the name of the Academy's Executive Committee was inadvertently misprinted. This has been corrected in the current issue. We apologize for the error.